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A general model of litter decomposition in the northern Chihuahuan Desert

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ABSTRACT

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Numerous empirical studies have described the pathways of mass, C and N flows during decomposition, but there remains a paucity of data on underlying mechanisms in arid ecosystems. In the northern Chihuahuan Desert, termites remove large quantities of litter and act as carbon and nitrogen sinks, contributing to low soil fertility. In their absence, decomposition at the soil surface is primarily driven by abiotic weathering, but studies suggest buried litter decay occurs through microbiological activities. We develop a general, synthetic model to examine the interactions between buried litter, decomposer microorganisms, and C and N pools in this ecosystem. Our goal is to explore the mechanisms underlying observed patterns of decomposition in arid systems using a modeling approach that balances simplicity with enough detail to suggest the reasons for system behavior. To this end, we utilize elements of existing models, interfacing microbial physiology and population dynamics with empirical observations of C and N pool dynamics, litter mass loss and changing C:N ratios. Good agreement was achieved between simulated and observed patterns of mass loss and nitrogen concentrations once a time lag describing the microbial colonization of litter was included. Model results indicate nutrient availabilities may be determined by relatively short-term carbon dynamics mediated by microflora since soil organic matter and nitrogen content are low. Model behavior also suggests decomposer organisms immobilize nitrogen from surrounding soils, accounting for the elevated quantities observed within decaying materials. Past hypotheses have proposed that soil flora and fauna partially decouple decomposition processes from abiotic constraints in this system. This study indicates that the pattern of microbial activities, accounting for the decomposition of buried materials in the absence of termites, is primarily determined by climatic conditions.

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INTRODUCTION

Although water availability has long been identified as the principal factor controlling productivity in arid ecosystems, recent studies have shown that nutrient limitations can be equally important in many of the drier regions of the southwest USA (Fisher et al., 1987, 1988; Gutierrez and Whitford, 1987a, b; Gutierrez et al., 1988). Since nutrient inputs are usually modest and soil fertility is low, dead organic matter is an important reservoir of nutrients. In the northern Chihuahuan Desert of southern New Mexico, low soil fertility is exacerbated by the very rapid loss of dead organic matter through two major pathways: (1) consumption of plant litter by subterranean termites, and (2) abiotic, physical-chemical degradation of exposed materials. Subterranean termites often consume the bulk of both above- and below-ground dead plant biomass (Johnson and Whitford, 1975; Whitford et al., 1982; Silva et al., 1985; MacKay et al., 1987; Whitford et al., 1988) and transport these materials to depths well below the rooting zones of most plants, thereby functioning as both carbon and nutrient sinks (Parker et al., 1982; Zak and Whitford, 1988). In the absence of termites, abiotic mechanisms may explain most surface litter disappearance (Silva et al., 1985; Montaña et al., 1988; Zak and Whitford, 1988), accounting for ca. 50–75% of the total annual loss of surface litter (Moorhead and Reynolds, 1989a).

Persistent litter in this region is buried by the activities of wind, water and small mammals (Steinberger and Whitford, 1983; Whitford et al., 1983). Subsurface decomposition appears to be more rapid than surface litter decay (Santos and Whitford, 1981; Elkins and Whitford, 1982) and is qualitatively different (Parker et al., 1984; Santos et al., 1984; Schaefer et al., 1985), dominated by biotic rather than abiotic components (Moorhead and Reynolds, 1989b). Although the contributions of termites to buried litter disappearance are often unclear (Ettershank et al., 1980; Silva et al., 1985), microfloral and microfaunal activities have been found to be important. Decomposition rates have been significantly reduced by the applications of selective biocides, e.g., insecticides, fungicides or nematicides (Santos et al., 1981; Elkins and Whitford, 1982; Parker et al., 1984) and budget models constructed by Parker et al. (1984) to describe carbon (C) and nitrogen (N) flows between litter, bacteria, fungi and microfauna, suggested significant roles of these organisms in decomposition and nutrient cycling processes.

While these numerous empirical studies have described the pathways of mass, C and N flow during decomposition, there remains a paucity of data on underlying mechanisms of decomposition in arid ecosystems. In this paper we develop a general, synthetic model to examine the interactions

between litter, decomposer microorganisms, and C and N pools in the northern Chihuahuan Desert. Our general modeling approach is based on fundamental decomposition processes that have been described in theoretical work (e.g., Parnas, 1975, 1976) and in detail for many other ecosystems, e.g., semi-arid grasslands (e.g., Montaña et al., 1988; Parton et al., 1987, 1988; Montaña et al., 1988), hardwood forests (Melillo et al., 1982), and agroecosystems (Paul and Voroney, 1980; Paul and Juma, 1981; Van Veen et al., 1981, 1984, 1987; Bosatta and Berendse, 1984; Holland and Coleman, 1987; Hunt et al., 1989). While these efforts represent a broad range of formulations and objectives, close comparisons reveal many commonalties. Our goal is to explore the mechanisms underlying observed patterns of decomposition in arid ecosystems using a general modeling approach that balances simplicity with enough detail to suggest the mechanisms of system behavior. To this end, we utilize elements of existing models, interfacing microbial physiology and population dynamics with empirical observations and C and N pool dynamics, litter mass loss and changing system C:N ratios.

IMPORTANCE OF MICROBIOLOGICAL ACTIVITIES

Most studies of buried litter decomposition in the northern Chihuahuan Desert concern changes in fine litter mass but not nutrient content over time (perhaps due to the difficulties in analyzing litter bag samples infiltrated with soil). Without this information, it is difficult to assess the contributions of microbial organisms to decay since mass losses also occur by other means. Plant roots, being larger and sturdier than leaf material, are more readily separated from soil particles and thus offer a better opportunity for studying mass and nutrient interactions. Whitford et al. (1988) found that the total N concentration in dead roots of *Baileya multiradiata* increased from 7.14 to 8.23 g kg^{-1} (considerable mass loss occurred through termite grazing). Termites would not be expected to greatly alter litter nutrient concentrations since they physically remove materials from the vicinity. Therefore, the 15% increase in the N concentration of *B. multiradiata* roots probably represents the additional activities of microbial organisms. The magnitude of this increase compares very well to the 16% mass loss of *B. multiradiata* roots on adjacent, termite-free plots (N analyses not performed). In a comparable study, N concentrations in dead roots of *B. multiradiata* increased from 7.17 to 8.55 g kg^{-1} (19%) over an 18-month period, although termites were again responsible for most of the mass loss (Mun and Whitford, unpublished). Whitford et al. (1988) also reported N concentrations increasing from 7.69 to 10.18 g kg^{-1}

(32%) in dead grass roots (*Dithyrea wislizenii*; July–October) but mass losses of this litter were not available from termite-free sites.

A detailed study of mass and N dynamics of buried *Lepidium lasiocarpum* leaf and root litter was conducted by Parker et al. (1984). Nutrient concentrations of litter were adjusted according to the relative soil content of the litterbags and the nutrient characteristics of nearby soil cores. Results were highly variable but demonstrated N immobilization in the root litter and identified fungal biomass as the major component of this nutrient pool. In the only other study of this nature conducted in the northern Chihuahuan Desert, Moorhead and Reynolds (1989b) used inverted petri dishes to limit the infiltration of soil particles into samples of buried, creosotebush (*Larrea tridentata*) leaf litter. Soil inputs were essentially nonexistant so that direct analyses of litter nutrient content were possible. Results showed a 20% mass loss, concurrent with a 25% increase in total N concentration (14.08 g kg^{-1} to 17.62 g kg^{-1}). Since termites had been excluded from the litter, these changes were attributed to microbial activities.

In all of these cases, changing nutrient concentrations during decomposition suggest microbial activities. While many mechanisms contribute to mass loss, few will result in net nutrient immobilization. Studies, such as the one by Parker et al. (1984), have also shown that microfaunal populations in decomposing litter can be quite high but still represent a very tiny fraction of the system C and N. Although microfaunal activities affect C and nutrient flows (cf. Parker et al., 1984; Hunt et al., 1987, 1989), they are primarily channelled through the microorganisms. It is the microbial pool that usually represents the largest quantity of both elements, aside from the litter. It remains to elucidate the processes underlying the interactions between C substrate, principal decomposers and nutrients that ultimately result in mineralization.

MODEL DESCRIPTION

Various pools (i) of C and N are used in our model, representing dead organic matter, living microbial biomass, and soil N (see Fig. 1). Flows between these pools are driven by empirical relationships according to characteristics of the microbial community. There are four pools of dead organic matter, three of which are derived from plants: $i = 1$, labile materials with high N content and rapid decomposition rate; $i = 2$, cellulose and related materials with an intermediate decomposition rate and very little associated N; and $i = 3$, very slowly decomposing recalcitrant compounds, such as lignins, with moderate levels of physically associated N. Dead microbiota ($i = 4$) has a high N content and decomposes rapidly

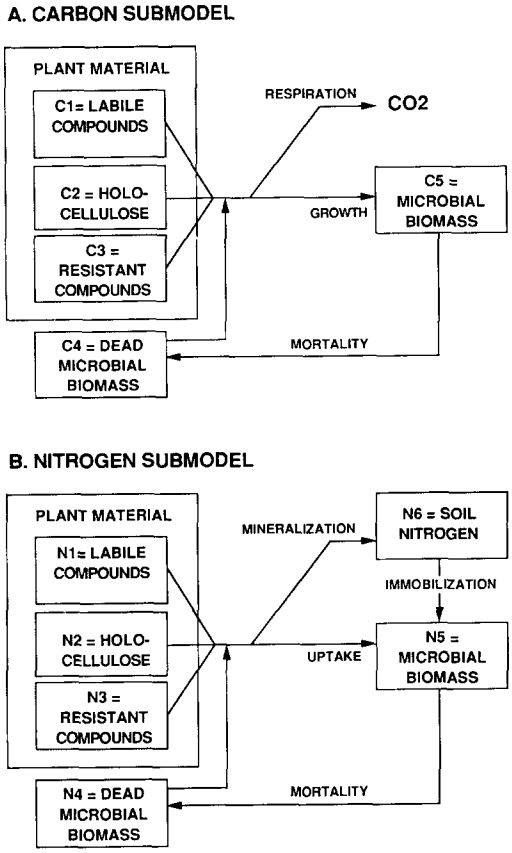

Fig. 1. Model flow diagram: A. carbon; B. nitrogen.

TABLE 1

Characteristics of carbon pools used in model simulations

Carbon pool	k [a]	[C:N] [b]	Percent [c]
C_1	0.20	5:1	11
C_2	0.08	1000:1	78
C_3	0.01	19:1	11
C_4	0.30	9:1 (5:1–13:1)	0
C_5	NA	9:1 (5:1–13:1)	0

[a] Fraction day^{-1} at 25 °C (Paul and Juma, 1981)

[b] Overall plant material C:N = 35:1 (see text for explanation)

[c] Total initial quantity of plant material = 1.85 g (Moorhead and Reynolds, 1989b)

TABLE 2

(a) List of parameters

Parameters	UA[a]	Equation	Value	Units	Explanation
[C/N]	✓	9, 10, 11, 12 2	See Table 1	gC/gN	Carbon : Nitrogen ratio
α	✓	2	0.311 (0.211–0.411)	unitless	Intercept of soil moisture effect on decay rate
b		14	0.0188	d^{-1}	Colonization rate
ϵ	✓	4, 6, 11, 12	0.6 (0.4–0.8)	unitless	Carbon assimilation efficiency
ϕ	✓	6	0.2 (0.1–0.3)	unitless	Growth-related microbial death rate
k		1, 4, 10		d^{-1}	Intrinsic decay rate
λ	✓	7	0.2031 (0.1031–0.3031)	$MPa^{-1}\ d^{-1}$	Slope of microbial water-shock mortality
μ	✓	2	0.345 (0.245–0.445)	MPa^{-1}	Slope of soil moisture effect on decay rate
Q	✓	3	2.5 (2.0–3.0)	$°C^{-1}$	Q_{10} value
Ω	✓	5	0.001 (0.0005–0.0015)	d^{-1}	Minimum microbial death rate

(b) List of state and auxillary variables

Variables	Equation	Units	Explanation
C	1, 4, 5, 6, 7, 9	gC	Carbon pools
C_a	4	$gC\ d^{-1}$	Litter carbon losses
C_{a*}	10, 11	$gC\ d^{-1}$	Potential carbon release from litter
D_1	5, 8	$gC\ d^{-1}$	Minimum microbial mortality
D_2	6, 8	$gC\ d^{-1}$	Growth-related microbial death
D_3	7, 8	$gC\ d^{-1}$	Microbial death due to water shock
γ	4, 6	$gC\ d^{-1}$	Microbial growth
I_{NET}	9, 11	$gC\ d^{-1}$	Net nitrogen immobilization
M	1,8	$gC\ d^{-1}$	Total microbial mortality
N	9, 13	gN	Nitrogen pools
N_{a*}	10, 12	$gN\ d^{-1}$	Potential nitrogen release from litter
N_{EXCESS}	13	$gN\ d^{-1}$	Total nitrogen available to microorganisms
N_{NEED}	13	$gN\ d^{-1}$	Microbial nitrogen need, corrected for mineral availability
$N_{STAT(i)}$	12, 13	$gN\ d^{-1}$	Internal nitrogen deficit in pool (i)
ρ	4	$gC\ d^{-1}$	Microbial respiration
$R_{N(i)}$	12	$gN\ d^{-1}$	Microbial nitrogen requirement to utilize potential carbon release from pool (i)
S_L	14	unitless	Effect of colonization lag on decay rate
S_M	1, 2, 4, 10	unitless	Soil moisture effect on decay rate
S_N	1, 4, 13	unitless	Nutrient-limitation effect on decay rate
S_T	1, 3, 4, 10	unitless	Temperature effect on decay rate

[a] Parameters selected for uncertainty analyses (range of values examined in parentheses).

TABLE 2 (continued)

(c) List of driving variables

Driving Variables	Equation(s)	Units	Explanation
T	3	°C	Soil temperature
t	14	day	Time
ψ	2, 7	MPa	Soil water potential

(see Table 1 for a summary of litter characteristics). The living microbial biomass ($i = 5$) represents the final pool of organic matter considered and the nitrogen submodel includes a soil N pool ($i = 6$). This compartmentalization scheme is comparable to the approaches of Paul and Voroney (1980), Paul and Juma (1981), Van Veen and Paul (1981), Parton et al. (1987), Jawson et al. (1989) and Stroo et al. (1989).

Carbon dynamics

Dead organic matter. The dynamics of the dead organic carbon pools through time (t) are given by:

$$(dC_i/dt) = -k_i C_i S_M S_T \, S_N(i) \qquad i = 1, 2, 3 \tag{1a}$$

$$(dC_4/dt) = -k_4 C_4 S_M S_T \, S_{N(4)} + M \tag{1b}$$

where C_i is grams of C in pool i; k_i is a maximum intrinsic decay rate; S_M, S_T, and $S_{N(i)}$ are scalar multipliers representing the effects of moisture availability (0–1), soil temperature (0–2.5), and N limitations (0–1), respectively, on decomposition rate; and M is total microbial mortality (see Table 2 for a summary of all variables and parameters). This approach is similar to Parton et al. (1987) but includes N limitations determined by balancing microbial energy and nutrient requirements (see below). The total quantities of C and N available for microbial use consist of the sum of all losses from the dead organic matter pools; the available N pool also includes mineral forms (assuming to be available to microflora).

Effect of soil moisture. In general, decomposition and microbial metabolic rates increase with increasing moisture availability, at least until saturation leads to anaerobic conditions (Wildung et al., 1975; Wilson and Griffin, 1975; Helweg, 1981; Stott et al., 1986). We use the approach developed by Paustian and Schnürer (1987) from data relating soil moisture to microbial respiration presented by Orchard and Cook (1983):

$$S_M = \alpha - \mu \log(-\psi) \tag{2}$$

where ψ is the soil water potential. This assumes maximum microbial activity at $\psi \leq -0.01$ MPa and minimum activity at $\psi \geq -8.0$ MPa. See Table 2 for parameter values.

Effect of soil temperature. Increasing temperatures usually increase the rates of microbial metabolism and decomposition, at least at temperatures below 30–40 °C (Wodzinski and Frazier, 1960, 1961a, b; Helweg, 1981; Hartel and Alexander, 1987; Parton et al., 1987). This relationship is most commonly described with a Q_{10} value that generally lies between 2 and 3, depending on the material being decomposed (e.g., Bunnel et al., 1977; Howard and Howard, 1979; Helweg, 1981; Stott et al., 1986). Therefore, we used a standard temperature response function ($T \geq 0$):

$$\log_{10}(S_T) = [(T - 25)/10] \log_{10}(Q) \tag{3}$$

where Q is the rate of increase (Q_{10}), T is soil temperature, and the value of S_T is set equal to 1.0 at 25 °C since the decay rate coefficients (k; Table 1) were observed at that temperature (exceeds 1.0 when temperatures exceed 25 °C).

Effect of nitrogen. Decomposition rates are also affected by such factors as nutrient and lignin content (cf. Meentemeyer, 1978; Melillo et al., 1982; Edmonds, 1987). Different materials decompose at different rates, and the maximum decay rate coefficient (k) of a particular material may serve as an index to quality (Table 1). In addition, the flow of C from nutrient-limited substrates (such as cellulose) is controlled by the availability of N from other sources. This is because the internal N content of such nutrient-limited pools is insufficient to meet microbial needs in association with potential C losses (based on k, S_M and S_T). Therefore, actual C losses from such materials are limited by balancing system C and N availabilities with microbial needs (see following description of system N dynamics) according to Parnas (1975, 1976) and Bosatta and Berendse (1984).

Microbial dynamics. Microbial dynamics are modeled as four basic processes: (1) growth, (2) respiration, (3) death, and (4) net mineralization or immobilization of N. It is the integration of observed decomposition patterns with microbial characteristics that provides the semi-mechanistic nature of this modeling exercise, and most clearly illustrates the intimate association between system C and N flows and microbial processes.

Microbial growth (γ) and respiration (ρ) are given as:

$$\gamma = \epsilon C_a \tag{4a}$$

$$\rho = (1.0 - \epsilon) C_a \tag{4b}$$

where ϵ is the assimilation efficiency, and C_a is total C available, i.e., total C losses from the litter:

$$C_a = \sum_i (k_i C_i S_M S_T S_{N(i)}) \qquad i = 1, 2, 3, 4 \tag{4c}$$

This assumes complete microbial utilization of C released from decomposing substrates in each time interval. Since C availability driving growth is limited by balancing microbial energy and nutrient requirements (see above), microbial growth is not nutrient-limited at this step. The dynamics of the microbial carbon pool is given by:

$$dC_5/dt = \gamma - M \tag{4d}$$

where M is microbial mortality (see below).

Microbial mortality. Many factors contribute to microbial death (Gray and Postgate, 1976; Henris, 1987) and three mechanisms are included in this model. First, a minimum fraction (Ω) of the standing biomass is assumed to die every day:

$$D_1 = \Omega C_5 \tag{5}$$

This is consistent with most other models of microbial populations that assume a minimum value for daily microbial turnover (e.g., Hunt, 1977; McGill et al., 1981; Van Veen et al., 1984).

Van Veen et al. (1984) actually use two daily microbial biomass turnover rates: 0.5% for a protected fraction of soil community, and 70% for the unprotected biomass. They define the protected fraction as the existing biomass of the soil given no recent soil disturbance or inputs of organic substrates. This is a clearly a specific characteristic of each soil and thereby difficult to generalize. However, this rationale also suggests that much of the system dynamics result from the rapid turnover of the unprotected fraction. Therefore, we assume that the daily incremental growth of the microbes roughly corresponds to the unprotected fraction of the soil biomass identified by Van Veen et al. (1984) and that a fairly large fraction (ϕ; Parnas, 1975) of this increment dies (D_2):

$$D_2 = (\phi/\epsilon)\gamma \tag{6}$$

Next, wetting-drying cycles have long been identified as a major factor stimulating biomass turnover (Lebedjantzev, 1924; Bhaumik and Clark, 1947; Stevenson, 1956; Wilson and Griffin, 1975; Lund and Goksoyr, 1980; Bottner, 1985; Schnürer et al., 1986; Hartel and Alexander, 1987). Orchard and Cook (1983) found as much as a 40-fold increase in microbial respiration rates when dry soil was wetted, and noted a linear relationship between the magnitude of this increase and the change in soil water

potential. Kieft et al. (1987) estimated that 17–58% of the total (i.e., 20–70% of the viable) soil biomass may be released by a rapid water potential increase, compared to 25–33% observed by Bottner (1985). Kieft et al. (1987) also noted that the fraction killed was proportional to the net change in ψ. We use a modified version of the Kieft et al. (1987) equation that yields a 30% biomass mortality (D_3) with a change in soil water potential from -1.5 to -0.01 MPa:

$$D_3 = \lambda(\psi_b - \psi_a)C_5 \tag{7}$$

where λ is the mortality associated with the change in soil water potential before and after wetting (ψ_b and ψ_a, respectively). Total daily microbial death rate (M) consists of the sum of all separate mortality rates:

$$M = D_1 + D_2 + D_3 \tag{8}$$

The appropriate slope and intercept of equation (7) depend on soil characteristics. Van Veen et al. (1984) discussed the importance of a soil's ability to protect a fraction of the microbial biomass from death induced by soil moisture fluctuations and Parton et al. (1987) suggested that the size of the protected community is greater in finer textured soils. This point is supported by the observations of Van Veen et al. (1987) in which a sandy-loam soil maintained smaller standing microbial communities and higher turnover than a clay soil. However, Kieft et al. (1987) found that the fraction of the biomass released by a drying–wetting cycle was greater in a silty clay loam than a gravelly loam soil. Clearly, factors other than texture are also involved so that actual size and response of the protected microbial community must be determined for any particular soil if a more accurate estimate of this relationship is necessary.

Nitrogen dynamics

The N dynamics of each dead organic matter pool ($i = 1, 2, 3, 4$) is set proportional to C dynamics by using a constant C to N ratio for each pool, $[C/N]_i$:

$$(dN_i/dt) = (dC_i/dt)[C/N]_i^{-1} \tag{9a}$$

The dynamics of the soil N pool is given by:

$$dN_6/dt = I_{NET} \tag{9b}$$

where I_{NET} is net immobilization and can be either positive (mineralization) or negative (immobilization). The flow of C from nutrient-limited substrates is controlled by the availability of N from other sources. This effect is given by the scalar $S_{N(i)}$ in equation (1) and is determined by

balancing C and N requirements of the decomposer microorganisms in three steps: (1) determine if the system N-limited and, if so, (2) determine how much N is available, and (3) estimate the realized decomposition rates for nutrient-limited substrates.

Computation of nitrogen-limitation scalar $S_{N(i)}$. Any existing mineral N (N_6) or N released from any substrate in excess of microbial need (required to utilize the C simultaneously released from the substrate) is assumed to be available for immediate microbial use in degrading N-limited substrates. For this step, *potential* C (C_{a*}) and N (N_{a*}) availability from dead organic matter is estimated by assuming no N-limitation (i.e., $S_{N(i)} = 1.0$; equation 1):

$$C_{a*} = \sum_i C_{a(i)*} = \sum_i (k_i C_i S_M S_T) \tag{10a}$$

$$N_{a*} = \sum_i N_{a(i)*} = \sum_i \left(k_i C_i S_M S_T [C/N]_i^{-1}\right) \tag{10b}$$

where $i = 1, 2, 3, 4$. We can now determine if the system is limited by N availability (Parnas, 1975, 1976; Bosatta and Berendse, 1984):

$$[C/N]_5/\epsilon = C_{a*}/(N_{a*} + I_{NET*}) \tag{11}$$

Case 1. If $[C/N]_5/\epsilon < (C_{a*}/N_{a*})$, then decomposition is N-limited and potential immobilization (I_{NET*}) of mineral N is positive.

Case 2. If $[C/N]_5/\epsilon > (C_{a*}/N_{a*})$, decomposition is C-limited and potential immobilization (I_{NET*}) is negative, i.e., mineralization of organic N may occur.

When the overall system is C-limited (case 2) or there is sufficient mineral N to meet the microbial demand ($N_6 \geq I_{NET*}$; case 1), there is no N-limitation to decomposition and all values of $S_{N(i)}$ (equation 1) are set to 1.0.

When the overall system is N-limited (case 1) and there is an insufficient mineral pool to meet microbial needs ($N_6 < I_{NET*}$), we estimate the extent to which the decay of each substrate is reduced. The amount of N required (R_N) to realize the potential decomposition of *each* substrate ($i = 1, \ldots, 4$) is computed from the relationship in equation (11), i.e.

$$[C/N]_5/\epsilon = C_{a(i)*}/R_{N(i)} \tag{12a}$$

thus

$$R_{N(i)} = C_{a(i)*}\epsilon/[C/N]_5 \tag{12b}$$

Next, the difference between $R_{N(i)}$ and potential N availability, i.e., $N_{a(i)*}$

(equation 10b), is computed to determine the N status of each pool ($N_{STAT(i)}$):

$$N_{STAT(i)} = R_{N(i)} - N_{a(i)*} \quad (12c)$$

$N_{STAT(i)}$ is positive for nutrient-limited substrates ($[C/N]_i > [C/N]_5/\epsilon$; cf. Parnas, 1975) and either zero or negative if not nutrient-limited ($[C/N]_i \leq [C/N]_5/\epsilon$).

The amount of N available (N_{EXCESS}) to support the decomposition of nutrient-limited substrates, the total amount of N needed (N_{NEED}) to realize potential decomposition, and the 0–1 scalar for nutrient-limited substrates (i.e., $S_{N(i)}$ are then estimated:

$$N_{EXCESS} = N_6 - \sum_i N_{STAT(i)} \quad (\text{for all } N_{STAT(i)} \leq 0) \quad (13a)$$

$$N_{NEED} = \sum_i N_{STAT(i)} \quad (\text{for all } N_{STAT(i)} > 0) \quad (13b)$$

$$S_{N(i)} = \begin{cases} N_{EXCESS}/N_{NEED}) & (\text{if } N_{STAT(i)} > 0) \\ S_{iN(i)} = 1.0 & (\text{if } N_{STAT}(i) \leq 0) \end{cases} \quad (13c)$$

This is the mechanism further controlling the loss of C from nutrient-limited materials (equation 1).

Net immobilization of mineral nitrogen (I_{NET}; equation 9b) is then estimated from equation (11) by replacing C_{a*} and N_{a*} with C_a and N_a and solving for I_{NET}.

MODEL SIMULATIONS

Initial conditions

We used this model to simulate the daily decomposition of creosotebush (*Larrea tridentata*) leaf litter, which has been previously examined by experiments conducted in the northern Chihuahuan Desert (e.g., Schaefer et al., 1985; Whitford et al., 1986; Moorhead and Reynolds, 1989b). The simulation period was 1 July through 18 October, corresponding to the field study conducted by Moorhead and Reynolds (1989b). Soil moisture and temperature regimes at 5 cm depth (the depth of litter burial by Moorhead and Reynolds) were provided by J. Cornelius (San Diego State Univ., CA, unpublished) and used to drive the model. Estimates mass losses and nutrient concentrations of the decomposing litter were compared to the results of the field experiment at all sampling dates to evaluate model performance. The pool of mineral N was considered zero at the start of simulations.

Since plant litter characteristics were not determined analytically by Moorhead and Reynolds (1989b), estimates were made as follows. Parton et al. (1987) identified two general plant litter components; structural and metabolic pools with C:N ratios of 150:1 and 5:1, respectively. Following this rationale, a combination of 15.5% metabolic and 84.5% structural materials produces an overall C:N ratio of about 26.7:1 as reported for senescent creosotebush leaf litter (Schaefer et al., 1985). This estimated metabolic pool size (15.5%) compares to a soluble content of about 17% reported for late-season, senescent creosotebush leaves (Conamor and Staffeldt, 1978). Since Schaefer et al. (1985) also reported a lignin content of 10.6%, the other structural component of *L. tridentata* leaf litter (i.e., hemicellulose and cellulose) was estimated at 73.9%. In addition, most of the N in the structural pool was assumed to be associated with the recalcitrant fraction (providing a C:N ratio of 19:1). Moorhead and Reynolds (1989b) soaked their litter in water before placing it in the field, which increased the C:N ratio to 35.5:1. The relative fractions of soluble, cellulose and lignin pools were then calculated by assuming the soaking removed part of the soluble component but quantities of cellulose and lignin were unaffected (Table 1).

Uncertainty analyses

Model uncertainty is defined as the relationship between variability in model predictions and the existing variabilities (or uncertainties) associated with parameter estimates. An uncertainty analysis was conducted to examine the sensitivity of model output to realistic variabilities in parameter values. Such analyses are useful in gaining a better understanding of underlying factors responsible for model behavior. Eight key parameters were selected for detailed examination (Table 2) and analyses conducted with PRISM, a computer program designed to perform Monte Carlo simulations for estimating uncertainty in model output (Gardner et al., 1983). This approach has been successfully used for a variety of models (e.g., Bartell et al., 1983; Gardner and Trabalka, 1985).

For each of the eight parameters, random samples were drawn from uniform frequency distributions within the range of values given in Tables 1 and 2. The model was run 100 times, each time with a randomly selected set of values for these eight parameters. Estimated mass losses and N concentrations for each sampling date were then analyzed to determine how much of the variability in model predictions was due to the uncertainty associated with individual parameter estimates. This was accomplished by obtaining the partial sums of squares attributable to each parameter

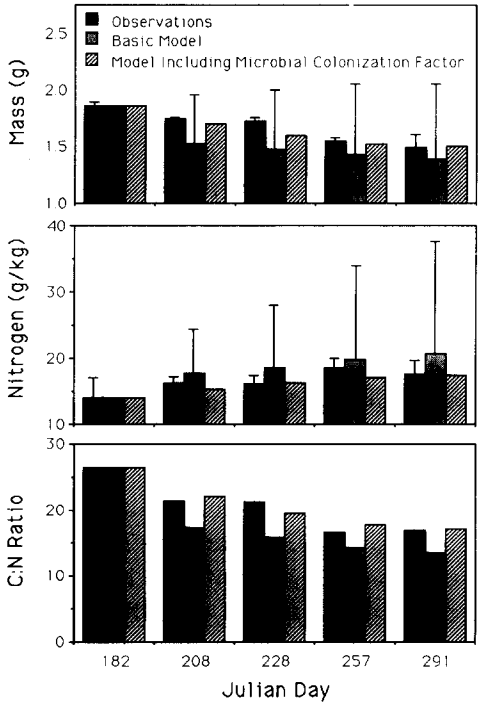

Fig. 2. Observed and simulated (mean $\pm$ 95% CI) *Larrea tridentata* litter characteristics (Moorhead and Reynolds, 1989b): dry mass (g); nitrogen concentration (g kg^{-1}); litter C:N ratio (twice the inverse of the mean nitrogen concentration). Basic model: without decomposition lag due to period of microbial colonization.

(PROC REG; SAS, 1985). The total partial sums of squares due to all model parameters and unexplained error sum to 1.0.

Results

Simulation results (shaded bars, Fig. 2) bracketed observed litter mass and N dynamics (black bars, Fig. 2) throughout the study period [the effect of microbial colonization (striped bars, Fig. 2) is discussed below]. On average, the model tended to overestimate mass losses, although differences between observations and estimates declined with time. Conversely, simulated N concentrations were usually greater than sample means. This is consistent with the overestimated mass losses provided by the model since N concentrations increase with C mineralization as long as N is conserved (as our model assumes). The large variation associated with model output (mass and N concentration) demonstrates the combined contributions of variations in the selected parameters (Tables 1 and 2) to

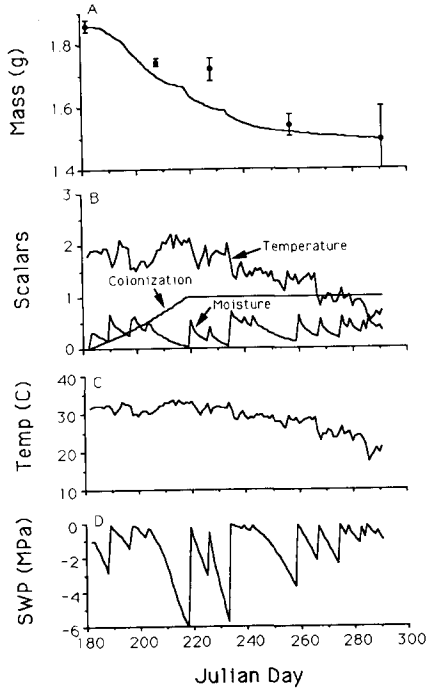

Fig. 3. Mass loss patterns and decomposition rate limiters: A. simulated (line) and observed (points; mean ± 95% CI) dry mass (g); B. scalar multipliers representing temperature, soil moisture content and microbial colonization effects; C. soil temperature at 5 cm soil depth during study period; D. soil water potential (SWP; −MPa).

model behavior. The model predicted no net mineralization of N throughout the simulation period. The C:N ratios of the litter samples were estimated as the inverse of twice the mean N concentration (assuming C contributed half the dry mass; Fig. 2). Comparison to simulated values again illustrates the results of overestimated C losses produced by the model (Fig. 2).

The effects of soil moisture (equation 2) and soil temperature (equation 3) on model behavior are illustrated in Fig. 3. Soil temperatures (5 cm depth) were probably close to biological optima (between 25 °C and 30 °C) throughout much of the study period (Fig. 3C), above the base temperature for which the relationship was established (25 °C; equation 3). Therefore, temperatures seldom limited decomposition rates. In contrast, soil water content was often very low (Fig. 3D), slowing decomposition rates (Fig. 3A, B) although wetting events at approximately days 218 and 234, following very dry periods, stimulated mass losses at these times (Fig. 3A).

In all cases, the uncertainties associated with the tested model parameters (Table 2) explained more than 99% of the variation in simulated mass

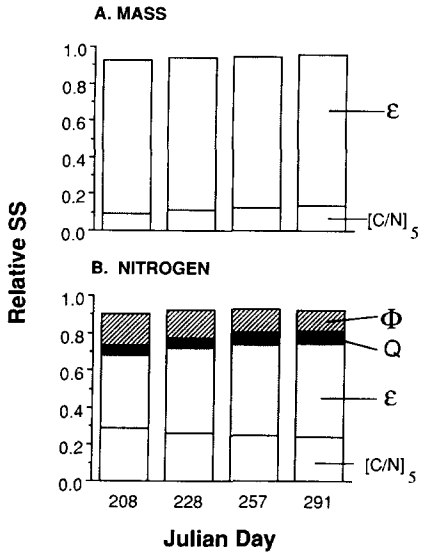

Fig. 4. Relative partial sums of squares resulting from uncertainty in individual parameter estimates: A. mass loss (ϵ, microbial assimilation efficiency; $[C/N]_5$, microbial carbon:nitrogen ratio); B. nitrogen concentration (ϕ, microbial growth-associated mortality rate; Q, temperature effect on decomposition).

loss values and more than 94% of the variation in simulated N concentrations. Most of the variations in mass were attributed to two microbial factors: C assimilation efficiency (ϵ), and [C:N] ratio (Fig. 4A). C assimilation efficiency accounted for over 82% of the total variation for all dates while [C:N] contributed ca. 9–14%. These two parameters were also the most important in explaining variations in simulated N concentrations, although the Q_{10} value describing the temperature response of litter decomposition rate and the microbial mortality associated with growth (ϕ) were also important (Fig. 4B). Overall, these results clearly indicate the importance of accurate estimates of certain model parameters. Of all, the assimilation efficiency and microbial C:N ratio have the greatest effect on model behavior.

DISCUSSION

Our general model appeared to reasonably mimic the observed system dynamics. This suggests that decomposition processes in soils of the northern Chihuahuan Desert are comparable to other ecosystems for which similar models have been developed from more extensive databases (e.g., Parton et al., 1987; Jawson et al., 1989; Stroo et al., 1989). Although litter

mass losses at the soil surface may be dominated by abiotic factors (Moorhead and Reynolds, 1989a), model results are consistent with the hypothesis that the disappearance of buried litter is primarily mediated by biological activities (Moorhead and Reynolds, 1989b). One of the obvious reasons for this difference in surface vs. subsurface decay processes is that the microclimate within the soil column is less extreme. Soil surface temperatures in summer often exceed the range for most biological activity (60 °C; Whitford and Ettershank, 1975). yet subsurface temperatures are more favorable (Fig. 3b, c). In addition, high sunlight intensities experienced by exposed litter are eliminated by burial. Finally, fluctuations in soil moisture regimes tend to diminish with depth (Moorhead et al., 1989), although the depth of litter burial in this study may have been too shallow (5 cm) to experience much difference from surface moisture conditions. The modification of these climatic characteristics with burial in the soil column both limits the importance of abiotic factors and enhances biological contributions.

Other studies have examined the roles of various C pools in total system dynamics and most decomposition models make some attempt to include different compartments of litter and soil organic matter (e.g., Paul and Juma, 1981; Parton et al., 1987; Stroo et al., 1989; Jawson et al., 1989). Since there are no comparable data for the northern Chihuahuan Desert, our model formulation included only the five compartments that seemed necessary to address the C–N interactions underlying decomposition (Fig. 1). Simulated C pool dynamics remain hypothetical, in the absence of detailed validation data, but provide estimates of these patterns based on whole system response (Fig. 5). Litter mass loss was initially dominated by labile compounds, followed by holocellulose, with relatively little of the recalcitrant fraction lost during the simulation (Fig. 5A). The live microbial pool clearly showed the effects of fluctuating soil moisture content (Fig. 5B) with wetting–drying cycles strongly affecting production (see Julian days 218 and 234). These results are consistent with those of similar studies of other systems (e.g., Hunt, 1977; McGill et al., 1981; Paul and Juma, 1981; Van Veen et al., 1984).

Total system N (the product of N concentration and mass remaining) was remarkably constant throughout the field study; increasing from an initial value of 26.2 to 28.5 mg by Julian day 257 and then decreasing to 26.3 mg by the final sampling date. This was consistent with the conservation of N in the litter–microflora complex simulated by the model. Denitrification and throughflow of soluble N compounds are probably limited by the overall dry conditions. In contrast, the total C:N ratio of the litter decreased from 35.5:1 to 28.4:1, representing a 20% loss of C relative to N (assuming C contributes approximately 50% of the dry mass). Microbial

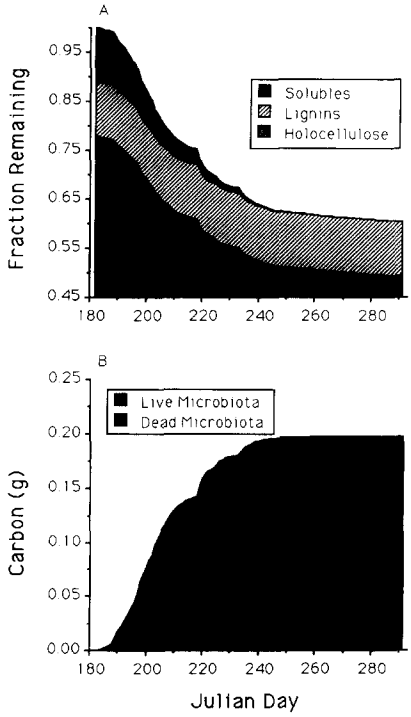

Fig. 5. Simulated carbon dynamics: A. litter carbon pools (relative fraction of initial litter carbon remaining); B. microbial carbon pools (g).

respiration and N immobilization could easily explain these patterns (as demonstrated by our model).

The uncertainty analyses identified the importance of microbial C assimilation efficiency (ϵ) and C:N ratio to model results (fig. 4), emphasizing the intimate association between C and N dynamics. A key relationship is the nutrient control of C mineralization, with microbial turnover providing the N required for utilizing holocellulose C; wetting–drying events increasing the turnover of microbial biomass (equation 7) and stimulated C mineralization (Figs. 3 and 5). Immobilization of N in microbial biomass has been identified as an important factor limiting productivity in the northern Chihuahuan Desert (Parker et al., 1984). Simulation results indicate that understanding N cycling in this ecosystem requires detailed knowledge of C cycling as well. Short-term decomposition processes may dominate the nutrient status of this system since it is not buffered by the presence of significant quantities of soil organic matter, accumulated litter or mineral nutrients.

The initial delay in actual mass loss (Fig. 2) suggested a lag in microbial activity, possibly corresponding to an initial period of colonization of the

litter by decomposer microorganisms (Zak, personal communication, 1990). We added a simple exponential function to our model in order to include this time lag:

$$S_L = (e^{bt} - 1) \tag{14}$$

where S_L is a scalar (0–1) applied to equation (1). A least squares curve-fitting procedure was used to select the value of the parameter b (0.0188) that provided the closest model estimates for both observed mass loss and N content. The period of microbial colonization reduced decomposition rates during approximately the first month of simulation (Figs. 3B) but ceased to be important after this point. Although the improvement in overall fit was modest, the estimated patterns of early mass and N dynamics were more consistent with observations (Figs. 2, 3A). The fact that incorporating a measure of the time lag in the microbial colonization of the litter provided a better correspondence between observations and simulations further suggests a central role of microflora in decomposition in this system. This is particularly evident since the temperature and moisture characteristics of the soil were as favorable during the first month of the simulation as any other period of the study although decay rates were low (Figs. 2 and 3).

Even our best-fit scenario (which included the microbial colonization period) tended to overestimate initial mass losses and underestimate N concentrations (Fig. 2). One of our original assumptions was that an external source of N was not available for microbial uptake. However, Parker et al. (1984) were often able to account for more N associated with buried, decomposing *Lepidium lasiocarpum* litter than was originally contained within the material. They attributed this to microbial (primarily fungi) uptake of N from surrounding soils and translocation to the vicinity of the decomposing litter. Holland and Coleman (1987) also observed this phenomenon during the decay of wheat straw, again attributed primarily to fungal activities. An external supply of mineral N would support higher nutrient concentrations in the decaying materials without demanding a proportional loss of mass, and permit a closer fit between simulated and observed patterns.

CONCLUSIONS

It was possible to approximate the mass and N dynamics of decomposing, buried litter in the northern Chihuahuan Desert, using a relatively simple model of microorganism–litter interactions. The results were consistent with microbe-mediated decay processes described by similar studies and models of other ecosystems; the effects of climatic driving variables

and changing litter quality were comparable. Model behavior also elucidated hypothetical relationships between C and nutrient dynamics, for which no validation data currently exist. In contrast to surface materials, the decay of buried litter in this desert appears to be controlled by microbiological activities. However, detailed studies of nutrient, C and microbial characteristics during decomposition are needed to verify this hypothesis.

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